

Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance'

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Large brain size in mammals has been related to the number and complexity of social relationships, particularly social alliances within groups. The largest within-group male alliance known outside of humans is found in a social network (>400) of Indian Ocean bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia. Members of this dolphin 'super-alliance' cooperate against other alliances over access to females. Males within the super-alliance form temporary trios and occasionally pairs in order to consort with individual females. The frequent switching of alliance partners suggests that social relationships among males within the super-alliance might be relatively simple and based on an 'equivalence rule', thereby allowing dolphins to form large alliances without taxing their 'social intelligence'. The equivalence model predicts that the 14 males in the super-alliance should not exhibit differences in alliance stability or partner preferences. However, data from 100 consortships do not support the equivalence hypothesis. The 14 males exhibited striking differences in alliance stability and partner preferences suggesting that the super-alliance has a complex internal structure. Further, within the super-alliance, alliance stability correlates with consortship rate, suggesting that differentiated relationships within the super-alliance are based on competition for access to females.

Keywords: dolphins; alliances; social structure

1. INTRODUCTION

(a) Alliance formation in Shark Bay

Indian Ocean bottlenose dolphins (*Tursiops aduncus*) form classic fission–fusion societies in which individuals associate in subgroups that often change in size and composition (Connor *et al.* 2000). In the Shark Bay (Western Australia) population, males form two nested levels of alliances. Males in pairs and trios cooperate to form aggressively maintained consortships with individual females for periods ranging from minutes to over one month (Connor *et al.* 1992a,b, 1996). Teams of pairs and trios form 'second-order' alliances that attack other alliances in contests over female consorts and defend against such attacks. Within this nested, functionally defined alliance structure are two patterns of alliance formation that may be extremes of a continuum, namely 'stable alliances' and the 'labile alliances', that comprise the super-alliance. Stable alliances are pairs and trios of strongly bonded males (association coefficients of 80–100) that may last for at least 14 years (Connor *et al.* 2000). Teams of two stable alliances (five to six individuals) cooperate in conflicts with other alliances and each stable alliance may maintain affiliative relationships with more than one stable alliance (Connor *et al.* 1992b).

The 14-member super-alliance is a very large second-order alliance in which members jointly attack other alliances (Connor *et al.* 1999). Within the super-alliance, trio formation is labile, as members often switch partners between consortships (Connor *et al.* 1999). Super-alliance males participate in five to 11 different alliances and have

five to 11 different alliance partners, all from within the super-alliance (comparable numbers are one to two and one to three, respectively, for males in stable alliances). The mean male subgroup size also differs significantly for super-alliance males and stable alliance males (6.1 versus 3.6) (Connor *et al.* 1999). The super-alliance home range overlaps extensively with those of three pairs of stable alliances (Connor *et al.* 1999).

(b) Alliance formation and social complexity

Complex alliances may be a manifestation of the 'social intelligence' associated with large brain evolution in primates and a few other mammalian taxa (e.g. Connor *et al.* 1992b; Harcourt 1992; Cords 1997). The triadic interactions between friends and foes that Kummer (1967) described within primate groups are more complex than the predictably hostile and, thus, comparatively simple interactions that may occur between groups (Connor *et al.* 1992a; Harcourt 1992). Alliance formation within some primate groups may be much more complex or 'strategic' than intergroup interactions, as individuals employ affiliative behaviour in order to recruit or compete for favoured allies (Harcourt 1992). Both levels of alliance formation among the bottlenose dolphins in Shark Bay occur within a larger social network of >400 individuals and are based on affiliative bonds (Connor *et al.* 1992a,b, 2000). However, there have only been a few observations of possible competition for alliance partners in dolphins (Connor *et al.* 1992b). The hierarchically nested structure of dolphin alliances may add an additional dimension to the complexity of their alliances (Connor *et al.* 1992a). In nested alliances, individuals must consider the impact of actions at both alliance levels rather than simply in their

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own alliance. Outside of humans and dolphins, nested within-group alliances are apparently rare, possibly explaining why nested alliances have not received more attention in discussions of social intelligence.

Shifting alliance partners is often cited as evidence of the strategic nature of primate alliances (e.g. Nishida 1983; Nishida & Hosaka 1996). Such shifts have been reported over short time-scales in interactions between stable alliances of bottlenose dolphins, over longer time-scales within stable alliances (Connor *et al.* 2000) and over short time-scales in an unstable alliance of three males that were provisioned with dead fish by a campsite (Connor *et al.* 1992a; Connor & Smolker 1995). Connor *et al.* (1999) suggested that frequent partner switching might be important in maintaining the structural integrity of the super-alliance. There may also be an important strategic component to the pattern of alliance shifts in the super-alliance. Alternatively, the frequent alliance shifts might represent the operation of a simple equivalence rule.

(c) *The equivalence model*

The equivalence model offers an explanation for how animals classify things whether they are perceptually similar or not (Sidman 1994). Schusterman *et al.* (2000) defined equivalence as 'relations between things, such as signals, objects, behaviors, or individuals, that become mutually interchangeable, or acquire meaning, through common spatiotemporal or functional interactions' (p. 1). Animals organize their perceptual world into equivalence classes and members of an equivalence class are interchangeable. The sight, sound and scent of potential prey may be interchangeable signals of one equivalence class for a predator. Similarly, in social contexts different individuals may be classified into different equivalence categories such as 'friend' or 'foe' (Schusterman *et al.* 2000). The simplest version of the equivalence model generates a parsimonious explanation for the shifting alliances within the super-alliance: individuals in the super-alliance treat each other as interchangeable members of an equivalence class. The implications are profound; alliances could be enlarged without requiring additional social intelligence or information processing as individuals would simply need to recognize others as being members of the same class (friend) or not being members of the same class (foe). This simple equivalence model predicts that members of the super-alliance will not exhibit partner preferences within the super-alliance.

2. METHODS

(a) *Field observations*

Observations of the super-alliance were made during 12 months (June–October) from 1995 to 1997 in Shark Bay, Western Australia. Data on male relationships were collected in two ways. We recorded the composition, location and predominate activity of any dolphin subgroups encountered during 'surveys'. Survey data were used to calculate home ranges and association coefficients between individual males found together with female consorts (Connor *et al.* 1999) using the 'half-weight' method (Cairns & Schwager 1987). During 'focal follows' on super-alliance members, individuals were observed for periods ranging from 1 to 8 h. Because observations were limited to days

with calm weather, we increased the number of surveys and follows by using two boats, each equipped with a video camera and hydrophone for recording behaviour and vocalizations. During follows, occurrences of specific behaviours were recorded onto a second audio track on the video recorder.

Alliances did not always have a female consort, but were still recognizable as alliances by their consistent association, side-by-side travel formation and synchronous surfacing. Nevertheless, here we only scored males as having formed an alliance if they were observed consorting with a female. A given alliance between males was considered to last for the duration of one consortship. For example, if the same three males had different females on consecutive days they would be scored for two alliances, whereas if they had the same female for three weeks they were scored for only one alliance.

Following Connor *et al.* (1996), a consortship was recorded if we observed (i) the female captured by the males, (ii) the female attempting to escape from the males, (iii) the males producing the 'pop' vocalization (see Connor & Smolker 1996), (iv) at least one of the males directing aggression at the female, (v) an attempted 'theft' of the female by other alliances, or (vi) the association between the alliance and the female for at least 1 h during follows or during multiple surveys spanning > 1 h.

(b) *Analysis*

Data on alliance membership were analysed using the SOCPROG program (Hal Whitehead, Dalhousie University, <http://is.dal.ca/~hwhitehe/social.htm>). A permutation test (10 000 permutations) (Bejder *et al.* 1998) was employed in order to test for preferred and avoided alliance partners for each of the 14 members of the super-alliance. An average linkage cluster analysis was performed on half-weight association coefficients in order to illustrate alliance associations within the super-alliance. The consortship rate for each of the 14 males was determined based on the percentage of days a male was observed in a consortship. An alliance stability index for each of the 14 males was calculated by dividing the number of different alliances a male participated in by his total number of consortships and then subtracting this number from one. This yields an index that ranges from zero for complete instability (a different alliance for every consortship) to almost 1 for complete stability (one alliance for all consortships) (the value will approach 1 as the number of consortships increases). In addition, we calculated indices for each male's fidelity to (i) a particular alliance, and (ii) his top alliance partner. Alliance fidelity and partner fidelity were simply the ratios of the number of alliances a male participated in with his most common alliance and common alliance partner, respectively, to his total number of alliances. In order to examine whether alliance stability is associated with the duration of consortships, we determined the proportion of each males' consortships that were observed for more than one day. Correlations were performed using SPSS 9.0 for Windows.

3. RESULTS

During 1995–1997 we documented 100 consortships of 35 females by super-alliance members (95 male trios and five pairs). Each female was involved in one to 14 consortships, most in only one of the three years, but four were consorted in two years and one in all three years. A total of 39 different male alliances in the super-alliance were recorded (Connor *et al.* 1999).

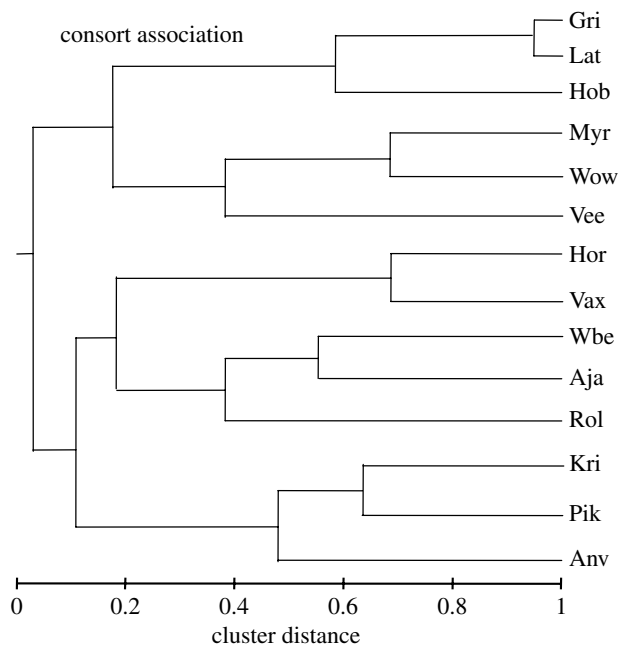


Figure 1. Average linkage cluster tree of alliance associations in the super-alliance based on half-weight association coefficients calculated from 100 consortships.

The predictions of the equivalence model were not met; the permutation test showed strong preferences and avoidances within the super-alliance (figure 1). Based on a two-sided significance level for dyads ($p > 0.975$ or $p < 0.025$), 42 significant dyads (16 preferences and 26 avoidances) were recorded whereas only four significant dyads were expected (5% of 91 possible dyads among the 14 males) (see Bejder *et al.* 1998).

Further, there was a significant correlation between the consortship rate and alliance stability for all 14 males (Spearman's rank correlation, $r_s = 0.838$, $n = 14$ and two-tailed $p < 0.001$) (figure 2). Three males in the super-alliance (Gri, Lat and Hob) (figure 1) formed the most stable alliance and had the highest consortship rates but the correlation remains significant when these males were removed from the analysis (Spearman's rank correlation, $r_s = 0.692$, $n = 11$ and two-tailed $p = 0.018$). Similarly, there was a significant correlation between alliance fidelity and the consortship rate (Spearman's rank correlation, $r_s = 0.812$, $n = 14$ and two-tailed $p \leq 0.001$) (figure 3a), which remained marginally significant with the removal of Gri, Lat and Hob (Spearman's rank correlation, $r_s = 0.647$, $n = 14$ and two-tailed $p = 0.031$). However, there was no significant correlation between the consortship rate and partner fidelity (Spearman's rank correlation, $r_s = 0.242$, $n = 14$ and two-tailed $p = 0.4$) (figure 3b). In fact, the male with the lowest consortship rate had the third highest partner fidelity but omitting him did not produce a significant correlation (Spearman's rank correlation, $r_s = 0.416$, $n = 13$ and two-tailed $p = 0.16$).

Finally, males that formed more stable alliances may have formed more enduring consortships. Twenty-nine of the 100 consortships were observed on more than one day. The proportion of multiday consortships was associated with alliance stability for the 14 males (Spearman's rank correlation, $r_s = 0.606$, $n = 14$ and two-tailed $p = 0.022$).

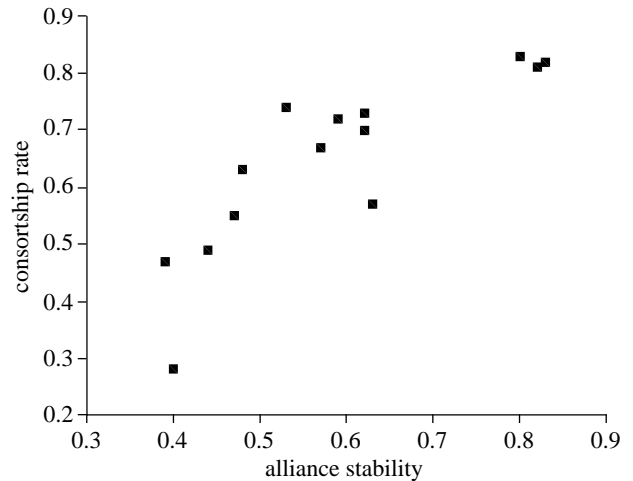


Figure 2. Scatter plot of consortship rate versus alliance stability for the 14 males in the super-alliance.

(figure 4a). This relationship could have been obtained simply by males that formed stable alliances being observed on more days, but they were not (Spearman's rank correlation, $r_s = 0.096$, $n = 14$ and two-tailed $p = 0.744$) (figure 4b).

We illustrate variation within the super-alliance with three males: a member of the most stable trio (Lat), a male with an intermediate consortship rate but highly variable alliance membership (Rol) and the male with the lowest consortship rate (Vax). Lat participated in 29 consortships but in only five different trios and had only six of the 14 males as alliance partners. All but one of Lat's consortships were with the male Gri (97%) and 55% were with the most consistent trio in the super-alliance, for which we also recorded the longest streak of consecutive consortships (ten). No other trio engaged in more than five consecutive consortships before disbanding. However, members of the most consistent alliance still participated in a total of five to six different trios. This was outside of the range of males in stable alliances (see Connor *et al.* 1999).

Rol participated in 23 consortships in 12 different alliances (11 trios and one pair) and had 11 out of the 14 males as alliance partners. Rol's most common trio accounted for only 17% of his consortships and his most common partner was present only 44% of the time. Rol participated in consecutive consortships with the same alliance only once.

The male Vax participated in only ten consortships (the fewest) in six different alliances with five different partners. Three of his ten consortships (30%) were in male pairs (only four other super-alliance males were recorded in pairs and no other male had more than 13% of his consortships in pairs). Vax was with the male Hor in nine of his ten consortships, but Hor did not reciprocate his faithfulness as he formed alliances without Vax eight times (45%).

4. DISCUSSION

The permutation tests of Bejder *et al.* (1998) (see also Whitehead 1999) offer a way of testing a simple equivalence

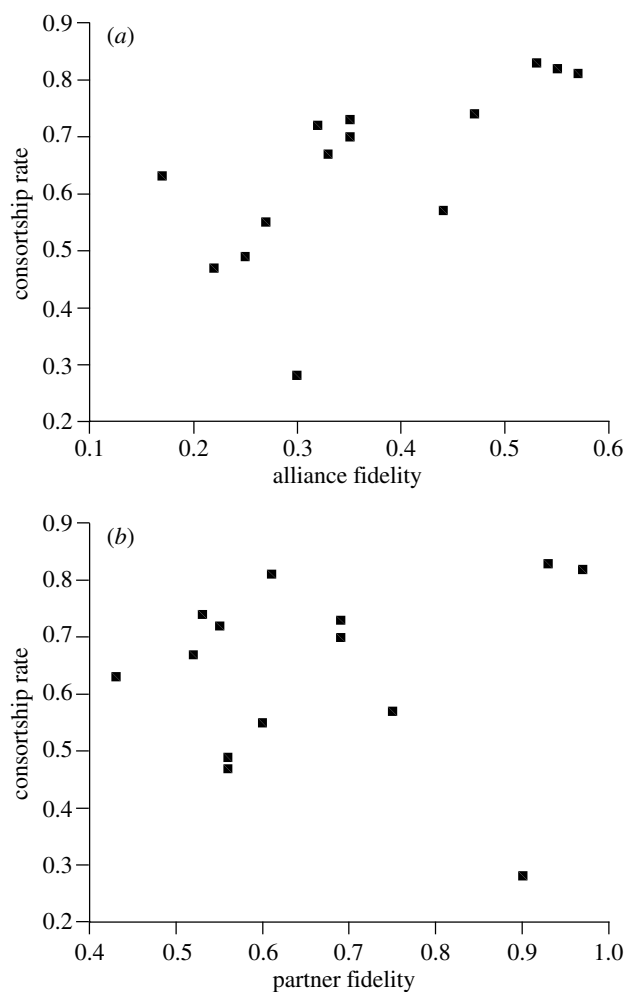


Figure 3. Scatter plots of consortship rate versus (a) alliance fidelity and (b) partner fidelity for the 14 males in the super-alliance.

model of social relationships. The frequently shifting composition of alliances within the super-alliance invites the hypothesis that members treat each other as interchangeable for the purposes of consorting females. However, they clearly do not; not only are there strong preferences and avoidances associated with alliance formation within the super-alliance, the stability of an individual's alliance membership correlates with the rate he consorts females. We therefore reject the simple equivalence model applied to relationships among males in the super-alliance. The data demonstrate that males within the super-alliance exhibit a more complex social structure, the basis of which is likely competition for access to females.

More complex equivalence models can be constructed that may reflect how animals categorize their perceptual world more accurately (Schusterman *et al.* 2000). For example, equivalence groups may have a hierarchical structure so there can be equivalence groups within equivalence groups (Schusterman *et al.* 2000). However, the equivalence model loses its appeal of parsimony in the process, so that, in the extreme case, where social relationships are individually differentiated, the equivalence hypothesis becomes simply a restatement of the observed—complex—pattern of individual relationships. Consider the nested stable

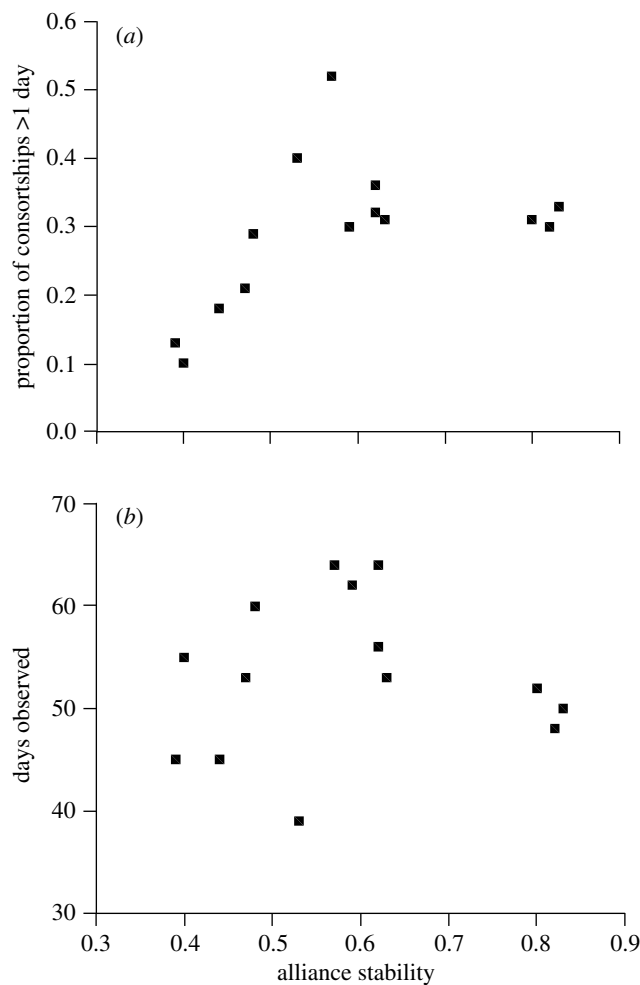


Figure 4. Scatter plots of the proportion of each male's consortships (a) lasting more than one day and (b) total days observed against alliance stability.

alliances; first- and second-order alliances can be considered as hierarchically arranged equivalence groups. However, there also, the pattern of shifting partnerships within and between alliances over time suggests that individuals and alliances are not interchangeable (Connor *et al.* 1992b, 2000). The equivalence model may be most powerful in its simplest form in which it offers a parsimonious explanation for patterns of social relationships that appear to be complex. In the case of nested dolphin alliances, the complexity is real.

Our findings have implications for the social intelligence hypothesis for large brain evolution. The social relationships of the super-alliance may compare with social relationships among a similar number of males in a primate group. However, unlike the males of a primate group, the dolphin super-alliance is embedded in a much larger society. Thus, the complexities of intragroup relations will apply to interactions that males have outside the super-alliance as well as within it. Although males in the super-alliance do not form alliances with males outside the super-alliance, they do occasionally associate with some of them during episodes of resting, travelling or socializing, including, on rare occasions, males from stable alliances that they have had conflicts with.

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